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CORRELATIONS BETWEEN ECOLOGY AND MORPHOLOGY IN ANOLINE LIZARDS FROM HAVANA, CUBA AND SOUTHERN FLORIDA

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No. 5 — *Correlations Between Ecology and Morphology in Anoline Lizards from Havana, Cuba and Southern Florida*

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INTRODUCTION

In many areas of the vast range of the iguanid genus *Anolis* several species occur sympatrically. There is, therefore, very good opportunity to analyze the ecological separation of sympatric species and to test the correlation of morphological with ecological differences. Almost no use has been made of this opportunity up to the present. Oliver (1948) has indeed discussed the ecology and morphology of *Anolis* on Bimini Ids. in the Bahamas but he did not expressly correlate the two. Lundelius (1957) appears to be the only worker who has carefully correlated ecological differences with morphology (in two fence lizards of the genus *Sceloporus*).

In the present paper an attempt is made to correlate morphology and ecology in five species of *Anolis* from Havana, Cuba. The possible effects of introduced *Anolis sagrei* on *Anolis carolinensis* in southern Florida are also assessed.

MATERIALS

Over the past seven years nine trips of one to two weeks' duration have been made to Havana, Cuba, to study the herpetofauna. Two of the trips were in early September and the remainder were in the period from December 19 to January 4.

Field observations have been made on more than twenty specimens of each of the following species: *Anolis angusticeps* Hallowell, *alutaceus* (Cope), *porcatus* (Gray), and *sagrei* (Dumeril and Bibron). The primary reason for using observations from a limited area was to eliminate effects of geographical variation. In addition, one specimen each of *A. argillaceous* Cope and *A. equestris* Merrem, as well as three specimens of an apparently new species of anole were taken. All observations on Cuban species (except *equestris*) are based upon specimens personally collected.

Additional specimens of *A. equestris* from other parts of the province of Havana were used to supplement the single specimen from the study area.

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THE STUDY AREA

The study area extends for about 1700 meters along the west shore of the Rio Almendares in the city of Marianao across the river from Havana. It is a low-lying strip no more than 200 meters wide. An abandoned road, the Carretera del Rio Almendares, runs most of the length of the area and crosses the river just below the Jardines de la Tropical. There is a fairly large field in the northern part of the area and some other smaller clearings in the woodland but most of the area is densely wooded. A cliff about 150 feet high separates most of the area from Marianao. There are some old ruins toward the southern end of the area completely shaded over by large trees. Figure 1 shows a stylized transect of the study area.

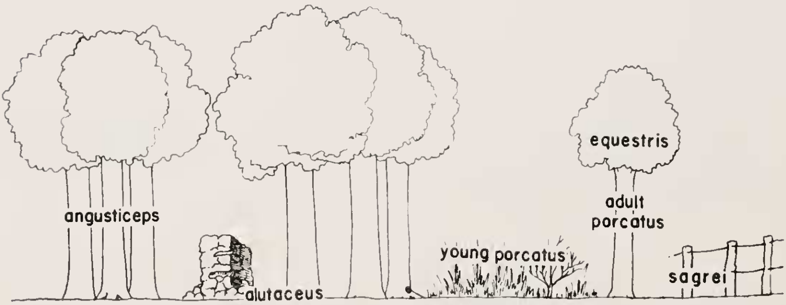

Fig. 1. Stylized cross-section through the study area showing the niche of five species of *Anolis* from Havana, Cuba.

THE SPECIES OF *ANOLIS* STUDIED

The ecology of each species of *Anolis* is described in this section from personal field observations in the study area with supplemental notes from the literature. Data are included on: where each species has been collected; background color; body color; method of locomotion; population density; and interspecies contacts.

Much of this information is summarized in Table I where the species are listed in order of increasing "arboreality." As here used, the more time an animal spends in a tree or the higher up in a tree it is, the more arboreal the animal is considered to be. This is an arbitrary method of distinguishing between habitats without recourse to the creation of a new complex terminology.

Anolis alutaceus (Cope). This small, slender, long-tailed anole is brown with a mid-dorsal tan stripe and a white dewlap. It is limited to a terrestrial niche in woodlands where it is found in three types of habitat: in holes and at the base of the walls of ruins; in rockpiles; and less often among the sticks and leaves of the forest floor. Almost half the specimens were taken on the ground and most of the others were in holes in the walls of the ruins. Three were seen or taken in trees. When approached while in holes, they may turn and retreat up to three feet into the hole or they may hop from the hole down to the ground. Once they land on the ground, they usually hop into the leaves and remain there, often with the head and most of the body hidden beneath the leaves. Part of the tail is usually visible if a careful search is made. One specimen was seen on the low branches of a tree and when chased it did not rely on its protective form and coloration as others have. It used its long hind legs to hop from branch to branch but did not make any attempt to run up, down, or along the branches. None have ever been seen attempting to climb up or down a wall.

An estimate of the relative abundance of *alutaceus* in the area of the ruins was obtained on good collecting days. From 9:40 to 11:55 A.M. on December 29, 1955, seventeen specimens were seen or captured. From 9:40 to 11:10 A.M. on December 23, 1958, six *alutaceus* were collected. There were scattered individuals on the ground elsewhere but they were more difficult to see and catch. No fighting was seen between individuals of this species but this may be due to the fact that they are not usually close together. In the ruins, they may be only a few feet apart, but they are in separate holes and cannot see each other. This species is limited to woodlands that are moderately damp and have a low light intensity. The few body temperatures available indicate that it is active at lower temperatures than the other species studied. Barbour and Ramsden (1919: 154) also report that *alutaceus* is confined to woodlands but note one unusual case of a specimen crossing a hot, dusty road. Within the study area, *alutaceus* comes into contact with *angusticeps* on the walls of the old ruins and with *porcatus*, to a much lesser extent, near the base of some cliffs.

Anolis angusticeps Hallowell. A short-tailed, short-limbed, long-headed anole which is gray or gray-brown with a pale peach-colored dewlap. In the study area, it is limited to a woodland habitat and 17 of 23 specimens were collected on tree trunks two to six feet from the ground. Three specimens were taken on the walls of the ruins and one was found on the ground. All were taken in moderately moist areas of low light intensity. Individuals rest on tree trunks with the head pointed upwards and when approached remain motionless for a short period but climb quickly if the first attempt to collect fails. Although temperatures were taken in the field on only four specimens, these show the preference of this species for cooler areas. Oliver (1948: 7) observed *A. angusticeps chickcharneyi* only on the upper branches of light gray-colored trees on Bimini, Bahamas. In the study area in Cuba, the species is found on gray or gray-brown tree trunks. Here the abundance of *angusticeps* varies from year to year. In 1957, five specimens were collected in 70 minutes on the morning of December 24 and five more in 30 minutes on the morning of December 27. In 1958, only two specimens were taken in two weeks of collecting. In the study area, *angusticeps* comes into contact with *alutaceus* on the walls of the ruins and with *porcatus* on tree trunks near the edge of the woodlands.

Anolis argillaceus Cope. Only one specimen of this small stocky lizard was taken in the study area. It was collected on December 24, 1957 at 10:35 A.M. among some vines in the crotch of a tree on the border of a clearing. When the vines covering the lizard were moved, the lizard tried to run back under cover rather than up the tree trunk as *porcatus* would, or down to the ground as *sagrei* would have done.

Barbour and Ramsden (1919: 149) report this species as confined entirely to eastern Oriente. This record constitutes a range extension to the west of almost 500 miles.

Anolis equestris Merrem. A large handsome lizard with the upper surface of the head developed into a magnificent bony casque. It is usually a brilliant green and both sexes possess a pink dewlap. The only specimen taken in the study area, a juvenile, was located at a height of six feet in a small tree in a field. Its habitat as noted by Barbour and Ramsden (1919: 133-135) and verified by Kane (personal communication) consists of orchards, palm groves, and trees along roads. None have been seen on the ground, and the majority of specimens have been seen at heights of more than 15 feet in trees. Both sources note fighting on the smooth trunks of the Royal Palm. Light and temperature intensity is greater in these habitats than in the woodland habitat of *alutaceus* and *angusticeps* and somewhat less than in the habitats of *sagrei* and *porcatus*. Kane (personal communication) collected one *equestris* that had partly eaten another anole but the specimen is not available for identification. In laboratory cages, I have observed mating and other behavior taking place most often on branches rather than on the cage bottom. In the study area, *equestris* can come into contact with *porcatus* and possibly *angusticeps.*

Anolis porcatus (Gray). A long-headed medium-sized anole which has a purplish-pink dewlap. It is found everywhere in the study area except in open fields and deep woodlands. Young are common on small bushes and in tall grass in areas of high light intensity. Adults are found on fence posts and tree trunks. The young are usually green and the adults are usually brown. Currently, it is the commonest lizard in the study area. However, since it is a species preferring edge areas, its great abundance is due in part to man who by breaking up woodland areas and planting trees in open areas, has created an ideal habitat for *porcatus.*

In the study area, *porcatus* seems to be most active in morning and afternoon with a period of decreased activity at midday. This has been noted by Oliver (1955: 133) for the related *carolinensis* during the month of April in Florida where it is most active from 8-11 A.M. and again from 4-6 or 7 P.M. *A. porcatus* probably spends the night in crevices or exposed on bushes or trees. Oliver (1955: 134) has noted this behavior for *carolinensis.* Collections made early in the morning revealed a high percentage of individuals under bark and in crevices in trees. Due to political conditions in Cuba, no collecting could be done at night but one specimen was observed asleep in the fold of a garden plant at night.

Although it is difficult to estimate the abundance of *porcatus* in the study area, the species seems to be found everywhere in favorable habitats. Some indication of its abundance may be gathered from the following field observations. On the trunk of a large fig tree six specimens were collected, and the population on the trunk from the ground to 15 feet up was estimated to be at least 20 lizards. After the first few are collected from one tree, the rest are disturbed, and it is almost impossible to catch all of them. They frequently congregate in large numbers in limited areas, a phenomenon not noted for the other anoles of the study area. For example, under a sign with an area of six square feet, at a height of seven feet above the ground, six to eight specimens were noted at 1:30 P.M. Numbers of *porcatus* may be collected in curled up fronds of broken palm branches that have lodged in another tree. At least 20-30 juvenile to adult *porcatus* along with one *Hyla septentrionalis* and one *Sphaerodactylus cinereus* were taken from one such palm frond. There were 15-20 in another curled up palm frond. When the palm frond was unfolded, the lizards immediately scurried off in every direction.

While territoriality has been noted for *carolinensis* in Bimini (Oliver, 1955: 111), in the study area, however, large populations found on single tree trunks in December seem to indicate that if territoriality occurs, it is not expressed to any considerable extent at this time of year.

During this study, only one anole was observed feeding. A small juvenile *porcatus* was seen sitting on a weed stalk about four feet from the ground in a clearing. It crept slowly toward the end of the stalk and grabbed a resting dragonfly.

In the study area, *porcatus* comes into contact with *sagrei* frequently on fence posts. It also meets *angusticeps* in areas bordering dense woodland and probably also contacts *equestris* farther up in trees.

Since specimens of *A. carolinensis* Voigt in the Cornell University Herpetology Collection from the Fort Myers-Bonito Springs area of southwestern Florida and from Key West were examined in order to study the effects of populations of *sagrei* upon *carolinensis*, a few remarks on this species are inserted here to provide a proper comparison with *A. porcatus*.

Anolis carolinensis Voigt. This species is native to the United States, is a smaller representative of the Cuban *porcatus*, and is probably correctly considered as conspecific with *porcatus* (Oliver, 1948: 12). I have observed this species only casually in North Carolina and in Miami, Florida. From these observations and from the literature, it is apparent that *carolinensis* occupies both terrestrial and arboreal habitats though perhaps preferring the latter. Duellman and Schwartz (1958: 279) give the optimum habitat in southern Florida as mesophytic hammocks, or in cultivated areas in gardens and shrubbery around houses. The dewlap is rose-pink to red and the body color varies within a wide range of browns and greens. Over most of its range, *carolinensis* does not come into contact with any other member of the genus. However, on Key West and around several cities in southern Florida, it does come into contact with introduced populations of *A. sagrei*.

Anolis sagrei (Dumeril and Bibron). This long-legged, short-headed, alert anole has an orange-red dewlap and can change color within a wide range of browns from pale tan to almost black. It is the common lizard of the roadside and open field. The juveniles and females are found mostly on the ground or a short distance from the ground among weeds. Adult males are usually found singly on observation perches at the top of woodpiles or on fence posts. Schwartz and Ogren (1956: 98), Barbour and Ramsden (1919: 143), Barbour (1904: 58, and 1914: 286), and Oliver (1948: 25) all report on its great abundance on the ground, brush, fallen logs, and boards, fence posts, and piles of debris. In the study area *sagrei* is second only to *porcatus* in abundance. Evans (1938) notes that *sagrei* males defend territories from other males of the same species; no attempt was made to verify this in the study area. However, two males were never taken on the same fence post and only rarely on the same telephone pole. When an attempt is made to approach *sagrei* on fence posts, they quickly retreat to the ground and swiftly run away. This has also been noted in the Cayman Islands by Grant (1940: 29) and on Bimini, Bahamas, by Oliver (1948: 25). The males always face downwards while on fence posts which indicates that their food is terrestrial. Evans (1938: 103) notes that they make frequent forays for insects in all directions from the observation perches on fence posts. My field observations show that *sagrei* becomes active somewhat later in the day than *porcatus* and has a peak of activity in the middle of the day. Collections from 8 to 10 A.M. have revealed that some individuals are partially active under rocks. They probably spend the night under rocks and other such cover. In the study area, *sagrei* comes into contact only with *porcatus* at the base of trees and fence posts.

Anolis sp. Three specimens of a medium-sized white-throated anole were also taken from the study area. They seem to resemble *A. carolinensis* most closely. Nothing is known of their ecology since they were not individually tagged in the field. They will be treated in a subsequent paper.

Associated Herpetofauna. Since they are part of the total ecology of the study area, the following list of herpetofauna is presented. Amphibians: *Rana catesbeiana* (one adult and many tadpoles of this introduced species taken in backwaters of the Rio Almendares); *Hyla septentrionalis* (common in holes in trees); *Eleutherodactylus atkinsi atkinsi, E. cuneatus, E. ricordii planirostris*[1] (abundant under rocks throughout the study area). Turtles: *Pseudemys decussata* (common on rocks in the Rio Almendares). Lizards: *Hemidactylus mabouia* (at night near

[1]These *Eleutherodactylus* were determined by Mr. Benjamin Shreve.

house lights); *Gonatodes fuscus* (on logs and trees); *Sphaerodactylus notatus* (under debris throughout the study area); *Sphaerodactylus cinereus* (under bark of trees throughout the study area); *Leiocephalus cubensis* (common in edificarian situations near the study area); *Amphisbaena cubana* (a few individuals under debris in open areas). Snakes: *Arhyton vittatum* (a few specimens under rocks); *Tretanorhinus variabilis* (a juvenile under a car tire on the river shore); *Alsophis angulifer* and *Dromicus andreae* (a few in a field several years ago before it became overgrown); *Typhlops lumbricalis* (fairly common under rocks); *Tropidophis maculatus* (few) and *Tropidophis pardalis* (common) (both species under rocks and other debris).

Most of these species probably have little effect on the *Anolis* in the study area. *Tropidophis* is the most important member of the associated herpetofauna since both *T. maculatus* and *T. pardalis* include *Anolis* in their diets. Both *A. alutaceus* and *A. angusticeps* have been found in the stomach of a *T. maculatus.* In the laboratory, both species of *Tropidophis* feed on *A. porcatus* and *A. sagrei* without hesitation. Captive *Alsophis* also feed on *Anolis* but these snakes are not present in large enough numbers to have much effect on the *Anolis* population.

SPECIES INTERACTION

Indications of fluctuations in populations of *porcatus* were noted within the study area over a period of a few years. The Carretera del Rio Almendares is lined, for part of its length, with fence posts. In the years when all the grass around the posts was cut down, *sagrei* was the most common lizard on the fence posts. In years when there was tall grass in the field behind the posts, and no grass along the road in front of the fence posts, some *sagrei* and some *porcatus* were present on the posts. In the last few years, some of the fence posts have taken root and furnish shade in the areas. With this change, *sagrei* has decreased and *porcatus* has increased in numbers on these living fence posts. In nearby areas, tall grass sometimes completely surrounds fence posts, and neither *sagrei* nor *porcatus* are present.

Although *sagrei* and *porcatus* are found on fence posts, they usually occupy different positions. Typically adult male *sagrei* are located facing downward on the lower part of the fence post no more than a few feet from the ground. On the same fence post, *porcatus* is found facing upwards on the upper part of the fence post. If one species is absent, the other will tend to occupy the entire fence post, but in all cases, *sagrei* faces downward and *porcatus* upward. In the Cayman Islands this has also been noted (Grant, 1940: 28) between *A. sagrei ordinatus* and *A. maynardi* (considered conspecific with *porcatus* by Barbour, 1937: 119). It is difficult to force *porcatus* to go down or *sagrei* to go up a fence post. When a line of fence posts was approached, each *sagrei* ran down the fence post into the leaves. A juvenile *porcatus* was observed to run to the top of a fence post and then to jump to two more fence posts in succession rather than move down the fence post. If placed on the ground, *porcatus* seems uncomfortable and it quickly moves to a nearby tree or fence post and climbs to safety. When approached by an observer, an adult *porcatus* which is on a tree will warily circle upwards around the tree putting the trunk between itself and the collector. This has also been noted by Oliver (1948: 16) for the related *A. carolinensis lerneri* on Bimini.

The Florida situation requires special attention. Populations of *sagrei* now exist on Key West and adjacent keys and in several mainland areas. The populations on the keys (*A. sagrei stejnegeri*) have apparently reached there by natural means. The mainland populations are recent introductions by man. Oliver (1950: 56) reports that Cuban *A. s. sagrei* have been introduced into the Tampa area. *A. sagrei ordinatus* have been introduced from the Bahamas into the Lake Worth area (Oliver, 1950: 56) and reported from Miami (Bell, 1953: 63). Duellman and Schwartz (1958: 283) refer the Miami populations to *A. sagrei stejnegeri*. Willis (1953: 74) reports *A. s. sagrei* from Coral Gables and Miami. At any rate, there are populations of the aggressive, terrestrial *sagrei* in contact with *carolinensis* in a number of areas in southern Florida. From studies by Oliver (1950), Neill (1951), Bell (1953), and Duellman and Schwartz (1958), it is apparent that the ecology of *sagrei* in regions of sympatry with *carolinensis* does not differ noticeably from *sagrei* in the study area in Cuba.

LAMELLAE

One of the most obvious differences in ecology of the *Anolis* species studied is relative arboreality (Table I). (See the definition above.)

The digital expansions of *Anolis* like those of geckos are undoubtedly adaptations to the generally arboreal habits of the genus. Differences in the extent of arboreal habit might consequently be expected to imply differing degrees of perfection and efficiency of these arboreal adaptations. Certainly the width of the digital expansion appears to correlate roughly with the degree of arboreality. However, this is a character difficult to make objective (See Fig. 2).

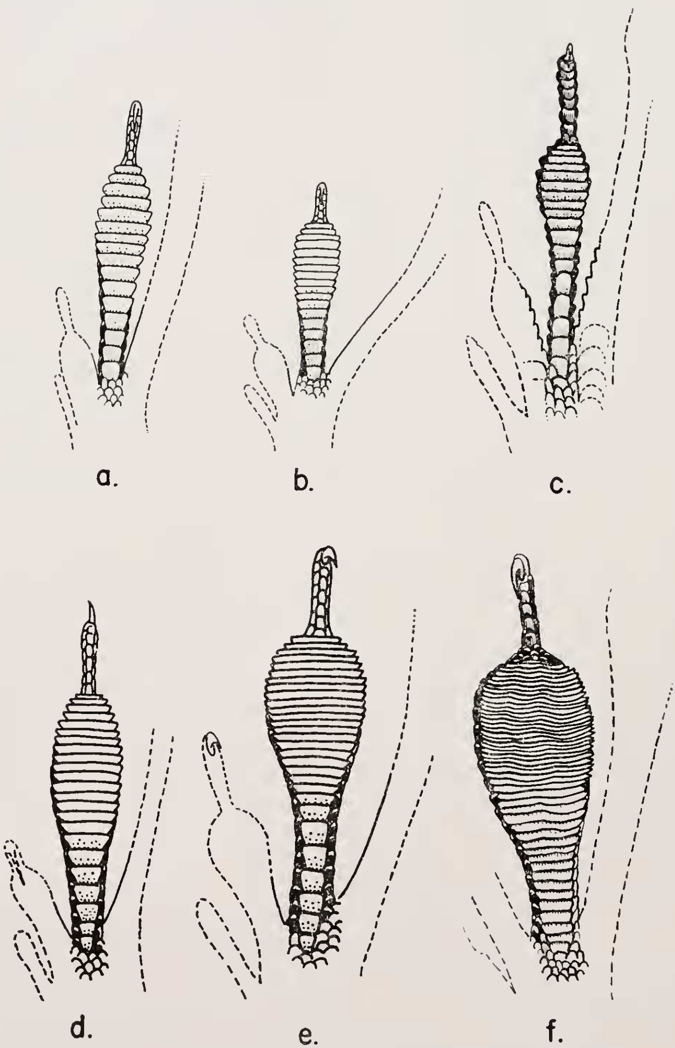

Fig. 2. Feet of six species of *Anolis* showing the lamellae on the third toe of the left hind foot. (a) *alutaceus*, (b) *angusticeps*, (c) *sagrei*, (d) *carolinensis*, (e) *porcatus*, (f) *equestris*. Not to scale.

Another conspicuous character of the digital expansion may, however, be quantitatively recorded — the number of lamellae. The correlations of this character have therefore been examined.

Counts were made of the lamellae of the third and fourth toes of the right front foot and the third toe of the right hind foot, of the *Anolis* from the study area, plus samples of *A. carolinensis* from Florida. These toes were selected because they have large numbers of lamellae and therefore seem to be important in bearing the weight of the lizard and are likely to show variation between species, and because counts can be made accurately since there is usually a distinct break between the lamellae of the toes and the scales of the foot. Counts were not made on the fourth hind toe because the distinction between lamellae and foot scales is less evident there. Enlarged lamellae-like scales on the foot were not counted. In the few cases where the proximal lamellae on the toes were divided, the divided lamellae were counted as one. Frequency distributions of the lamellae on each of the toes are presented in Tables II and III.

From the data thus obtained, three factors appear to be correlated with lamellae number. There is a positive correlation between lamellae number and body size(Table IV). This relationship is understandable because as the length of the lizard increases, the volume and presumably the weight increases as the cube while the area of the toes increases as the square. The increased number of lamellae in larger species compensates for the loss in toe area relative to weight. Hecht (1952: 118) has also shown a positive correlation between lamellae number and body size in species of *Aristelliger*. A second factor is that of sexual dimorphism. In the study area, except for *A. equestris* and *A. alutaceus*, male anoles have significantly more lamellae than females (Table IV). But this too may be a function of size since (except for the two species mentioned above) male anoles are larger than females (Table IV).[1] However, this rule does not appear to apply to Key West *carolinensis* in which, despite the larger size of males, there is no significant difference in lamellae number between males and females. Unless there is an ecological difference between males and females, this is difficult to explain. Thirdly, there appears to be a correlation between number of lamellae and arboreality as it has been defined above. The more arboreal species have more lamellae (Table IV). However, here

[1]But see ♀ *angusticeps* compared with ♀ *sagrei* below.

also there is some ambiguity. In general the more arboreal anoles are also larger.[1]

Increased numbers of lamellae could be ascribed wholely to the larger body size of arboreal species. However, there are several lines of evidence that suggest that there may be a real rather than a spurious correlation between arboreality and number of lamellae.

In *A. porcatus*, the young are found in a bush-grass habitat while adults are limited to a fence post-tree habitat. Superficial examination indicates that the toes become wider with age but more data is needed. There is no evidence of changes after hatching in lamellae number. The possibility of the phenomenon of

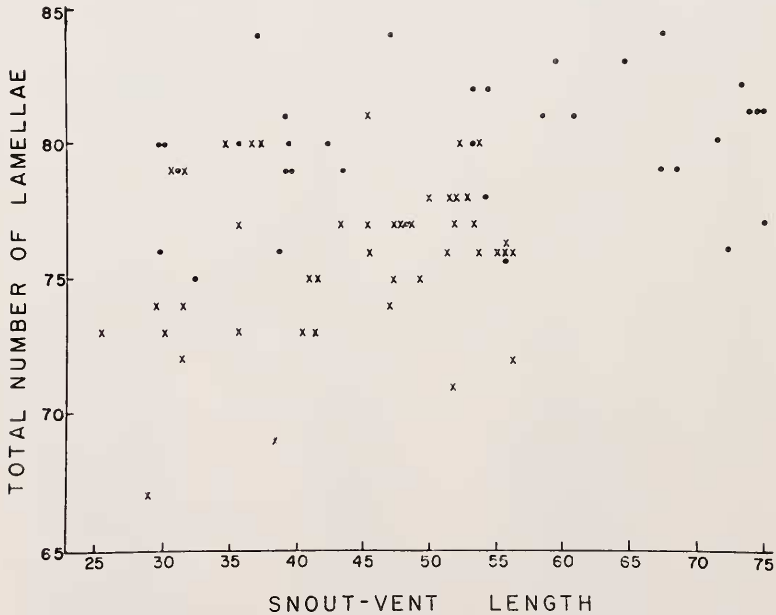

Fig. 3. Total number of lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of *Anolis porcatus* from Havana, Cuba. The dots represent males and the crosses females.

[1]Within a lizard genus, the more arboreal member of a group of sympatric species tends to be the larger. Within the study area, *porcatus* is larger than *sagrei*; *angusticeps* is larger than *alutaceus*; and *equestris*, the most arboreal of all, is the largest one. Studies in progress on the gecko *Sphaerodactylus* also show the arboreal *cinereus* to be larger than the terrestrial *notatus*. Smith (1946: 204, 222) has shown that the arboreal *Sceloporus olivaceus* is larger than the terrestrial *S. undulatus*. The significance of this trend is difficult to see.

wider variability in juveniles than in adults was tested in two ways. The total number of lamellae on the three toes counted was plotted against snout-vent length (Fig. 3). Until sex was taken into consideration, it appeared that the mean number of lamellae did increase with size classes, as found by Hecht (1952: 117) in *Aristelliger*. But this was due primarily to sampling bias. There are more males in the largest size groups and more females in the smallest size groups so the differences in mean numbers of lamellae are mostly an expression of the number of each sex in a given size group.

Specimens of *A. porcatus* for which both exact ecological data and lamellae counts are available fall into two ecological niches: (1) bushes and grass; (2) fence posts plus trees. For both sexes there is an increase in body size from the first to the second group (Table V). The mean number of lamellae in the bush-grass habitat is significantly lower than that for the fence post plus tree habitat. Thus, with a shift in habitat, there is a change in the distributions of body size and lamellae number which seems to be due to selection acting against individuals with low lamellae numbers. Selection acts not when a certain size is reached, but when the young make the habitat shift to fence posts and trees.

If lamellae number is plotted against snout-vent length for *sagrei*, a similar picture is obtained (Fig. 4). The main difference between the lamellae-body size relations in the two species is the greater separation between males and females in *sagrei*. However, only the male *sagrei* make a habitat shift, while in *porcatus* both sexes shift. Therefore, part of the male-female difference in *sagrei* may be due to the larger maximum size that the male reaches but part of it may be correlated with the fact that adult male *sagrei* are found on fence posts while the females and juveniles of both sexes are limited to life on the ground.

Comparison of female *angusticeps* with female *sagrei* also supports the correlation of arboreality with increased numbers of lamellae. Female *sagrei* are larger (mean 34.5mm, max. 44.4mm) than *angusticeps* (mean 32.5mm, max. 38.9mm) but *angusticeps* females have a larger mean and maximum number of lamellae. Female *sagrei* are almost completely terrestrial WHILE FEMALE *angusticeps*, LIKE THE MALES, ARE ARBOREAL.

A fourth case bears on the question of climbing ability and lamellae number. *A. carolinensis* of Florida is closely related to the Cuban *porcatus* and since it has no anole competitor over

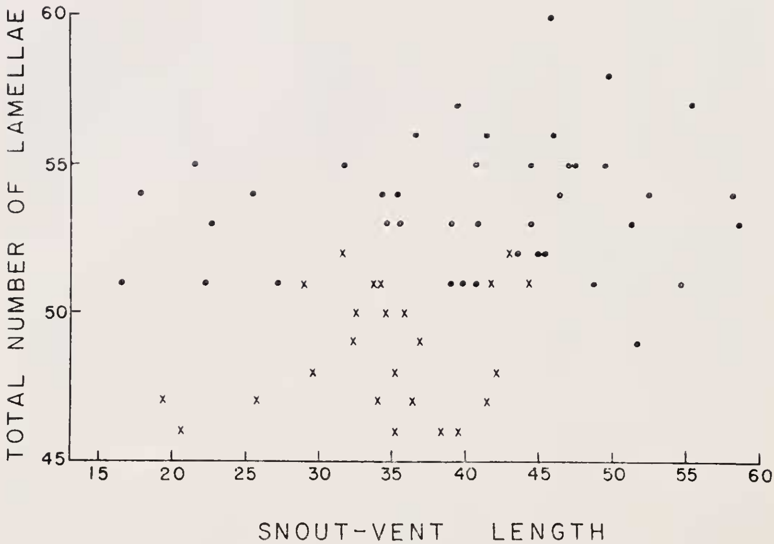

Fig. 4. Total number of lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of *Anolis sagrei* from Havana, Cuba. The dots represent males and the crosses females.

most of its range it is able to occupy all suitable anole habitats, both terrestrial and arboreal. Both in lamellae number and body size it is intermediate between two Cuban species — the arboreal *porcatus* and the terrestrial *sagrei* (Table IV). As discussed above, *sagrei* has become established in a number of areas where *carolinensis* is present. Theoretically the aggressive, terrestrial *sagrei* should tend to drive the more generalized *carolinensis* out of the terrestrial part of its habitat. There then should be strong selective forces favoring those *carolinensis* with higher lamellae numbers, since they can better utilize the arboreal part of the habitat. Counts on a small series of *carolinensis* from Key West, an area of long contact with *sagrei*, are indeed higher than counts from an area where they are not in contact (Fort Myers-Bonito Springs), as shown in Table IV. These differences are significant at the 99 per cent level for males and females (t values of 2.85 and 4.67 respectively). This is not conclusive evidence that the suggested theory is correct because there is the possibility that the lamellae numbers are correlated with greater body size, geographic variation in the latter character being the controlling factor. Evidence for or against the theory can only be obtained from study of *carolinensis* over a period of years in an area where *sagrei* has been recently introduced.

TAIL LENGTH

Tail length was measured to the nearest tenth of a millimeter from the vent to the tip of the tail. All specimens were carefully examined and individuals with broken or regenerated tails were excluded. Tail length was then divided by snout-vent length. *A. alutaceus* has a much longer tail than the other species studied (Fig. 5). This seems to be correlated with its use as a balancing

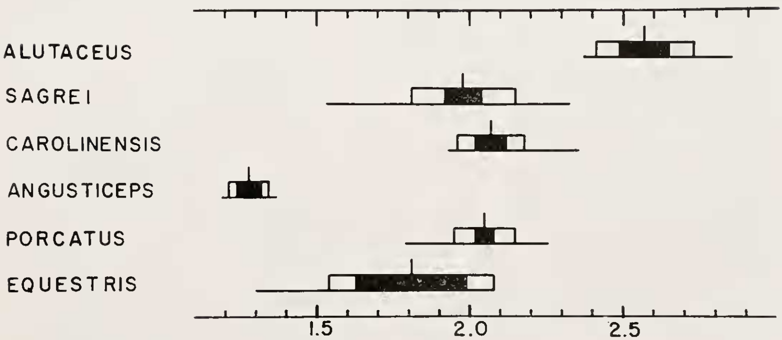

Fig. 5. Ratio of body length to tail length in six species of *Anolis*. The horizontal line represents the range, the vertical line the mean, the filled-in rectangle two standard errors on each side of the mean, and the open rectangle one standard deviation on each side of the mean.

organ as this species hops along the forest floor. *A. angusticeps* has a much shorter tail than the other species, possibly correlated with the slow deliberate movements of this species. The other tree-trunk dweller, *porcatus,* has a longer tail than *angusticeps.* possibly because as a juvenile it makes daring leaps from leaf to leaf and uses its tail as a balancing organ. All the arboreal species have the base of the tail somewhat thickened for use as a prop in climbing. This adaptation is not found in the terrestrial *sagrei* and *alutaceus.* The tail of the former is compressed while that of the latter is rounded and slender, well adapted for holding up in the air as a balancing organ while the lizard hops.

HIND LEG LENGTH

Hind leg length was measured to the nearest tenth of a millimeter from the anterior insertion of the thigh to the tip of the toenail of the longest toes with the leg extended at right angles to the body. Dividing hind leg length into snout-vent length provided the ratio on which comparisons were based. The larger arboreal species have shorter legs (Fig. 6). They move about

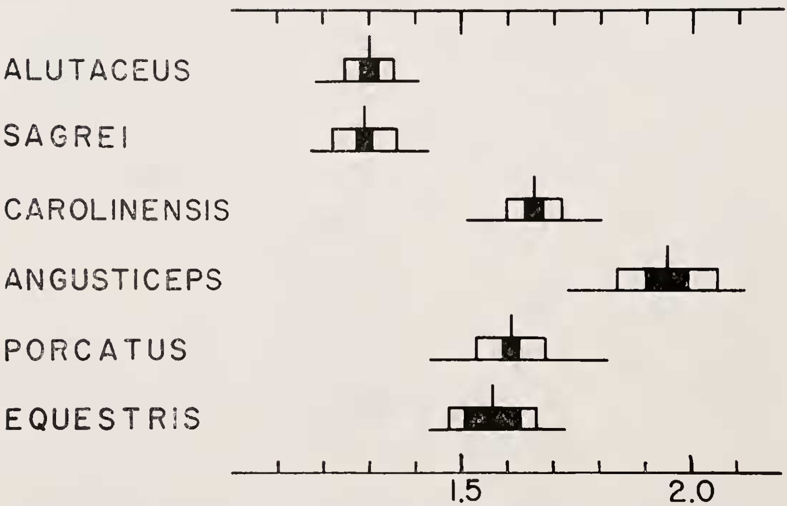

Fig. 6. Ratio of hind leg length to body length in six species of *Anolis*.

more slowly in the trees than the terrestrial species do on the ground. The long-legged terrestrial *sagrei* runs swiftly about in fields while the long-legged *alutaceus* employs its long hind legs in hopping on the forest floor. Lundelius (1957 : 80) reported that the terrestrial *Sceloporus undulatus* has longer legs than the arboreal *S. olivaceus*.

COLOR

Another adaptation to be considered is the ability of *Anolis* to change color. The two terrestrial species, *sagrei* and *alutaceus*, are limited to color and pattern shifts within a range of browns. The ability to turn green would be of no positive advantage against their brown backgrounds and would be selected against.

The arboreal *angusticeps* varies within a range of grays, gray-browns, and gray-greens, the colors which are present on the tree trunks of its damp woodland habitat. *A. porcatus* and *carolinensis* have the ability to change color within a wide range of greens and browns. Young *porcatus* are found among the leaves of shrubs and bushes where they are usually green. Adults are usually found on the trunks of large trees in diffuse daylight where they are usually brown.

The range within which a species can change color thus appears to be adaptive to their ecological niche (Table I). Hadley (1929: 110) notes that *porcatus* is green at night, brown in diffuse daylight, and green in direct sunlight. Color changes are primarily associated with changes in light, temperature, humidity, and emotional state, but in most cases they result in the lizard matching its background in nature (Van Geldern 1921: 81-87). An exception is found where bright green *porcatus* (and *carolinensis* in Florida) stand out against the brown of telephone poles and isolated trees in situations modified by man. But perhaps this is a habitat only recently colonized so there has been little time for selection to act and few predators to provide selection pressure.

As for the completely arboreal *equestris*, both Kane (personal communication) and Barbour and Ramsden (1919: 134) indicate that this species is normally green. Hadley (1929: 112) notes that *equestris* is normally green in diffuse light, the most frequent condition in its niche.

PERITONEAL PIGMENTATION

Differences in the distribution of black pigment in the peritoneal cavity are present in the species of *Anolis* studied. Black pigment is almost completely lacking in *alutaceus*. All the rest have at least a pigmented parietal peritoneum. In *angusticeps*, additional pigment is sometimes present on the ventral mesentery that suspends the liver. Both *porcatus* and *carolinensis* have additional pigment on the mesocolon and mesoduodenum. The latter also has pigment on the ventral mesentery of the liver. The pigment distribution is similar in *equestris* but does not extend into the most anterior portion of the peritoneal cavity. There is still more pigment in *sagrei*; it covers the entire large and small intestines and extends onto the testes of the male.

Oliver (1948: 28) has noted similar conditions in the Bimini *A. angusticeps chickcharneyi, carolinensis lerneri,* and *sagrei ordinatus,* but offers no suggestions as to the possible significance of these differences. There would appear to be a rough correlation of the amount of peritoneal pigmentation with the amount of radiation to which the lizard is exposed. The species of the deepest woodland, *alutaceus*, lacks pigment and the other woodland species, *angusticeps*, has only a slight amount. The three species of more open areas, *equestris*, *carolinensis*, and *porcatus*, are exposed to greater radiation intensities and have more pigmentation. *A. sagrei* prefers open fields and has the most pigmentation. It is possible that this pigmentation serves as protection against harmful solar radiation as Klauber (1939: 77) has proposed for reptiles in the southwestern United States. Even though Bodenheimer (1954) and Hunsaker and Johnson (1959) have indicated that the skin of some reptiles is impervious to various forms of radiation, no alternative to Klauber's explanation has yet been proposed.

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SUMMARY

This paper has attempted to correlate ecology with morphology in six species of *Anolis* from southern Florida and Havana, Cuba. It is felt that with proper ecological data, valid correlations can be made that can lead to an appreciation of the significance of characters often used in taxonomic analysis. Also, light is shed upon the structural adaptations that allow related sympatric species to occupy the same geographical area without facing deleterious competition. It has been shown that selection has acted so that lizards will usually match the color of their natural

background. Examples have been shown to support the idea that peritoneal pigmentation is connected with exposure to radiation. The value of long legs to terrestrial lizards has been shown. Short relative tail length has been correlated with arboreality. The more arboreal members of a group of sympatric species have been shown to be larger and have more lamellae than terrestrial species. Data have been presented to support the contention that increased numbers of lamellae are an adaptation to increased arboreality.

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TABLE I

Summary of ecological data for six species of *Anolis* from southern Florida and Havana, Cuba. The species are listed down the page in order of increasing arboreality.

Species	Habitat	Background Color	Body Color
alutaceus	On the ground or in holes in walls	Brown	Brown
sagrei	On the ground but adult males frequently on fence posts, etc. near the ground	Brown or gray	Brown-gray
carolinensis	In trees and on the ground	Green; brown	Green; brown
angusticeps	On tree trunks	Gray	Gray-brown
porcatus	Young — in bushes and grass Adults — on tree trunks and fence posts	Green Brown	Usually green Usually brown
equestris	High up in trees	Green	Green

TABLE II

Frequency distributions of the lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of females of six species of *Anolis* listed across the page in order of increasing arboreality.

							Mainland			Key West											
Species	*alutaceus*			*sagrei*			*carolinensis*			*carolinensis*			*angusticeps*			*porcatus*			*equestris*		
N		15			24			11			9			14			44			7	
Foot	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H
Toe	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3
No. lamellae																					
12			4																		
13	4		6																		
14	10		5			1															
15	1	2		4	5	8							3		2						
16		9		10	4	10							8		7						
17		2		7	13	3	1	1	2	1		2	2		3						
18		2		3	2	2	4	1	4	1		—	1	7	2						
19							5	6	3	1	2	4		6							
20								3	2	5	3	3		1							
21										1	3					1					
22											1					1	1				
23																5	—	1			
24																14	6	7			
25																14	13	10			
26																7	11	16			
27																1	10	8			
28																	2	2			
29																	1				

TABLE II (cont.)

35	1		
36	—	1	
37	—	1	
38	—	1	
39	3	1	1
40	2	—	1
41	1	2	1
42		1	1
43			1
44			1
45			1
46			

TABLE III

Frequency distributions of the lamellae on the third and fourth toes of the right front foot and the third toe of the right hind foot of males of six species of *Anolis* listed across the page in order of increasing arboreality.

Species	*alutaceus*			*sagrei*			Mainland *carolinensis*			Key West *carolinensis*			*angusticeps*			*porcatus*			*equestris*		
N		9			41			22			14			8			34			3	
Foot	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H	F	F	H
Toe	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3	3	4	3
No. lamellae																					
13	3		1																		
14	6		8																		
15																					
16		3		3	1	5							1		1						
17		4		8	9	15	1						6		7						
18		2		20	13	15	3		5	2	1	4	1								
19				8	16	4	12	6	11	2	5	2		3							
20				2	2	1	4	8	2	7	2	5		4							
21							2	7	3	2	3	2		1							
22								1	1	1	2	1									
23											1					1					
24																6					
25																5		4			
26																15	4	9			
27																5	16	11			
28																2	11	6			
29																	3	4			
35																			1		
36																			—		
37																			1	1	
38																			—	—	
39																			—	—	
40																			—	1	
41																			1	—	2
42																				1	—
43																					—
44																					—
45																					—
46																					1

TABLE IV

Correlation between body size and lamellae number in six species of *Anolis* from southern Florida and Havana, Cuba. The species are arranged down the page in order of increasing arboreality.

Species	Sex	N	Body Length	$\overline{X}$	Lamellae Number	$\overline{X}$	Variance	"t" value between sexes
alutaceus	♀♀	15	16.1- 39.4	29.23	40- 46	43.13	2.41	N.S.
	♂♂	9	16.0- 36.6	30.92	42- 46	44.44	1.53	
sagrei	♀♀	24	19.4- 44.4	34.47	46- 51	48.75	4.28	10.67**
	♂♂	41	16.5- 58.6	40.69	49- 60	53.66	5.03	
carolinensis (Mainland of Florida)	♀♀	11	27.4- 44.3	38.61	51- 58	55.91	3.20	3.19**
	♂♂	22	40.5- 56.5	49.42	55- 64	58.55	5.69	
carolinensis (Key West)	♀♀	9	44.3- 50.5	46.32	56- 64	60.67	6.50	N.S.
	♂♂	14	42.7- 59.1	54.16	55- 66	61.14	9.36	
angusticeps	♀♀	14	17.1- 38.9	32.51	49- 54	51.00	2.31	4.36**
	♂♂	8	34.1- 42.1	38.66	53- 56	53.63	0.99	
porcatus	♀♀	44	25.4- 56.4	44.24	67- 81	75.84	9.16	6.49**
	♂♂	34	29.7- 75.1	52.45	75- 84	79.97	5.61	
equestris	♀♀	7	83 -161	117.3	112-126	120.14	22.81	N.S.
	♂♂	3	149 -154	151.3	113-125	120.00	39.00	

** significant at the 99% level

TABLE V

Change in distributions of total number of lamellae and body size with habitat shift in *Anolis porcatus* from Havana, Cuba.

	Bush-Grass Niche					Tree-Fence Post Niche					
	Snout-vent length			Lamellae No.		Snout-vent length			Lamellae No.		
	N	Range	$\bar{X}$	Range	$\bar{X}$	N	Range	$\bar{X}$	Range	$\bar{X}$	"t" value
♀♀	6	29.0-56.4	38.4	67-77	73.0	18	31.4-56.0	45.4	71-81	76.2	3.24**
♂♂	6	29.7-48.4	36.6	75-81	77.3	15	35.7-75.1	55.8	77-84	80.7	2.22*

* significant at the 95% level
** significant at the 99% level